Influence of Elk Grazing on Soil and Nutrients in Rocky Mountain National Park

By

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Abstract. We used three 35-year exclosures to examine the effects of high elk populations on a variety of soil properties in three vegetation types: upland sagebrush, aspen, and meadow. Grazing and hoof action by elk significantly increased bulk density (from 0.87 kg/L ungrazed to 0.94 kg/L grazed), with greater effects on soils with fewer rocks. Grazing substantially reduced extractable calcium, magnesium, potassium, and phosphorus in the upland sagebrush type, but not in the aspen or meadow types. The only grazing effect on pH came in aspen vegetation types, where grazing prevented aspen establishment, and kept soil pH about 0.7 units higher than under aspen inside the exclosures. Grazing had no overall effect on total soil C and N across all exclosures and vegetation types, but soils from grazed portions of upland shrub areas had lower concentrations of extractable cations and phosphorus. The availability of soil nitrogen, indexed by in-field resin bags and net mineralization in soil cores, showed little overall effect of grazing. Limited data on soil leaching indicated a possibility of strong increases in nitrate leaching with grazing for an aspen vegetation type at one exclosure. Although we found little effect of grazing on soil N supply, we note that N fertilization doubled the production of grasses and shrubs; if grazing eventually led to changes in soil N supply, species composition and growth would likely change.

Keywords: Cervus elaphus, ecosystem processes, elk, grazing, mineralization, nitrogen, soil nutrients.

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Introduction

The population of elk (*Cervus elaphus*) has varied dramatically in the Front Range of the Rocky Mountains in Colorado. Intensive hunting extirpated elk in the late 1800s, but populations rose quickly following reintroduction in the early 1900s. Across the park, elk use varies by location and season. Areas of heavy grazing (particularly winter range for elk) show a lack of regeneration of aspen (Baker et al. 1997; Suzuki et al. 1999). The increases in elk populations, and concentrated areas of elk use, resulted from the elimination of all large predators (other than cougars), elimination or abbreviation of migration routes, and habituation of elk to humans and managed pastures, hay stacks, lawns, and golf courses.

Problems caused by overabundance of large mammals have concerned wildlife managers and scientists for decades (Caughley 1981). Traditionally, species were considered to be excessively abundant if high population densities reduced harvested yields, or if they caused unacceptable changes in the structure and composition of plant communities (Caughley 1981). For several reasons, these traditional approaches have been problematic. Approaches that define acceptable abundance in terms of harvestable yield focus narrowly on one species, and ignore effects of that species on other plants and animals. Defining desirable levels of abundance in terms of structural changes in plant communities may allow populations to reach undesirable levels before such changes can be detected (Caughley and Lawton 1981). Challenges in defining "harm" have prevented consensus [see reviews in Wagner et al. (1995) and Coughenour and Singer (1995)]. Basic ideas about density-dependent regulation of animal populations at equilibrium levels have also been questioned (Ellis and Swift 1988). These issues provide a problematic context for the discussion of "natural regulation" of herbivore populations by food supply, as currently practiced by the National Park Service in Yellowstone, Rocky Mountain, Grand Teton, and several other large western national parks (Wagner et al. 1995).

Grazing by domestic livestock typically alters soil organic matter, pools and turnover of nitrogen, and soil erosion, but these effects vary widely among locations (Risser and Parton 1982; Milchunas and Lauenroth 1993; Burke et al. 1997). Livestock impacts may be concentrated in some areas by fences, salt blocks, and supplemental water sources. Heavy livestock grazing compacts soil, reduces soil moisture up to 60%, lowers infiltration rates, creates a drier microclimate, and accumulates less litter (Knapp and Seastedt 1986; Fuls 1992).

The effects of wild, migratory ungulates on ecosystems may differ from those of domestic livestock. Wild populations of ungulates typically vary spatially and temporally in response to seasonal migrations and long-term population trends. In many cases, ideas and expectations about the nature and magnitude of grazing effects go far beyond the experimental tests available. Some sites are grazed only during the winter period when plants are dormant or for periods of only a few weeks during the growing season (McNaughton 1983; Frank and McNaughton 1992). Native ungulates may increase plant productivity, at least in the short term, by increasing nitrogen in forms that are more available to plants. Grazing may reduce root biomass and thus decrease the microbial biomass, thus reducing C:N ratios and making nitrogen more available to plants (Holland and Detling 1990; Seagle and McNaughton 1992). Herbivore feces and urine also provide large inputs of soluble nitrogen to plants (Risser and Parton 1982; Bazely and Jefferies 1985; McNaughton 1990). As a result of increased availability of nitrogen in a readily usable form on grazed sites, plant uptake of nitrogen is higher, leading to higher plant tissue concentrations of nitrogen (Moss et al. 1981; McNaughton 1983; Coughenour 1991; Singer 1995; Singer and Harter 1996). Tissue concentrations of nitrogen might be elevated above levels critical for overwinter survival of ungulates (Mould and Robbins 1981). Ungulates prefer to graze on regrowth from previously grazed sites, which leads to improved body condition and higher reproductive success (Moss et al. 1981; Iason et al. 1986; Gordon 1988; McNaughton 1988).

How substantial are the effects of elk on soils in the Rocky Mountains? Frank and Groffman (1998) examined soil properties inside and outside seven 2-ha exclosures that were in place for about 30 years, all in grass-dominated ecosystems in Yellowstone National Park. The net mineralization of soil nitrogen (N) was higher outside all seven exclosures than inside, with an average difference of about 2-fold. Four of the exclosures had substantial shrub cover, and no simple pattern of grazing impact was found. Shrubs at two exclosures showed no differences with respect to grazing, one had higher N mineralization under shrubs outside the fence, and the other higher N mineralization under shrubs inside the fence.

We assessed the impacts of heavy elk use on N using three large elk exclosures that have excluded elk and deer (but not small herbivores) for 35 years. We examined soil bulk density, total carbon (C) and N, as well as the minerals calcium (Ca), magnesium (Mg), phosphorus (P), and potassium (K), soil pH, available N, N-limitation on plant growth, and N leaching losses from the soil. The complete absence of ungulate grazing inside the exclosures is an artificial condition, given the long-term presence of ungulates in the region, so the gradient in grazing impacts between inside and outside the exclosures may be larger than would be found between typical ungulate populations and the current high-density situation.

Site Description and Methods

The three long-term elk exclosures are located in the Beaver Meadows area of Rocky Mountain National Park at an elevation of about 2,500 m. The climate is dominated by long, cold winters (average January temperature, -1° C), and sunny summers with frequent storms (July average temperature, 17° C). Precipitation averages about 41 cm/yr, distributed fairly evenly throughout the year with about half falling as snow.

The Estes Valley elk population was about 3,000 in the late 1990s (Lubow et al., this volume). In winter, about 70% of the elk stay within the town of Estes Park, and 25% to 30% reside inside the park. Grazing impacts are heavy in the lower valleys over winter and during spring and fall migrations to and from high-elevation summer range.

Exclosure 1 (0.4 ha) contains an upland sagebrush (*Artemisia tridentata*) community with scattered gooseberry (*Ribes inerme*), ponderosa pine (*Pinus ponderosa*), and grasses (*Bouteloua gracilis*, *Koeleria macrantha*, and *Muhlenbergia montana*). Exclosure 2 (1.2 ha) encompasses three vegetation types: upland sagebrush, mid-slope aspen (*Populus tremuloides*) with some scattered willows (*Salix monticola*, *S. geyeriana*, and *S. planifolia*), and lower-slope wet meadows dominated by sedge (*Carex* spp.) and grass (*Calamagrostis canadensis*). Exclosure 3 (0.4 ha) has two vegetation types: aspen and a mesic meadow (*Poa pratensis*, *Bromus inermis*, and *Phleum pratense*).

We stratified each exclosure into major vegetation types and sampled inside and outside the exclosures to determine the effects of elk grazing. Ten soil samples (6.2 cm diameter by 30 cm length, divided into two 15-cm intervals) were collected (in April 1999) at 2-m intervals along transects within each vegetation type and exclosure, and along paired transects that ran parallel to the fence lines. The transect locations were chosen 5–10 m away from the fence, in areas with matching microtopography. These samples were analyzed (by methods in USDA Natural Resources Conservation Service 1996) for bulk density (oven-dry basis), pH (2:1 water:soil paste), extractable phosphorus (Bray-1), and 1 M ammonium acetate-extractable calcium, magnesium, and potassium.

Available N was assessed by two methods, using the same sampling design as the soil samples. Net N mineralization was estimated with the closed-top-core technique (Adams and Attiwill 1986). Plastic tubes were pounded 15 cm into the mineral soil and capped for incubation periods ranging from 4 weeks (summer 1998) to 6 weeks (autumn 1998) to 6 months (winter 1998–1999). After the incubation period, soils were collected, mixed, and 10-g subsamples were extracted for 24 hours with 100 mL of 2 M KCl; ammonium-N and nitrate-N were determined on a Perstorp automated colorimeter. Net N mineralization was calculated as the post-incubation concentrations of ammonium and nitrate minus the concentrations from paired cores taken at the beginning of each incubation period. About one-third of the net mineralization rates were negative, and these values were set to 0 (representing no N available to plants for that sample location and period). The net N mineralization rates were summed across periods to give an annual estimate.

Ion exchange resin bags (Binkley and Hart 1989) were also used to estimate the availability of ammonium-N and nitrate-N. Resin bags were constructed with two sections: one with anion resin (14 mL of Sybron IONAC ASB-IPOH), and one with cation resin (14 mL of Sybron IONAC c-251 H^+). Each section of the resin bag was about 4 x 4 cm, with a band of heat-applied glue separating the pouches. In each vegetation type in each exclosure, 10 bags were placed 2 cm below the mineral soil surface, at 2-m intervals along a transect in May 1998, and retrieved in October 1998. A second set of resin bags was installed in October 1998 and retrieved in May 1999. In the laboratory, the anion and cation resin pouches were combined and extracted with 100 mL of 2 M KCl. Concentrations of ammonium and nitrate were determined colorimetrically on a Perstorp autoanalyzer.

We assessed the nitrogen limitation on plant growth by fertilizing small 2-m radius plots (12.5 m^2) with 10 g N/m^2 as urea, in March 1999. Two plots were fertilized in each vegetation type, inside and outside each exclosure. The extent of N limitation was evaluated by the length, mass, and N content of the 25 largest new shoots per shrub in July 1999 and by clipping herbaceous biomass from 0.25 m^2 plots.

The losses of N from the soil were estimated with porous cup lysimeters (2-cm diameter cups at 30–35 cm depth) in the wet meadow vegetation type for exclosure 2 and for the aspen vegetation type in exclosure 3. All the other exclosure and vegetation types were too rocky to insert lysimeters. Ten lysimeters were installed inside and outside at each site. The soils were too dry or frozen for sampling soil leachate except in the spring following snowmelt and major storms. On May 3, 13, 24, and June 22, 1999, water samples were collected from the lysimeters by applying a suction (-1 MPa), and returning several hours later to collect the accumulated water. Samples were stored in a cooler (2–4° C) for up to 5 hours before freezing for later analysis by automated colorimetry. Nitrogen concentrations were averaged across three sampling periods for each site. The variances of the soil solution concentrations were not normally distributed, so we used a non-parametric Kruskal-Wallis comparison to test for the effect of grazing.

We analyzed the effects of grazing three ways. We used *t*-tests to compare all samples within each exclosure with all samples outside that exclosure. We also used *t*-tests to compare individual vegetation types at each exclosure. These *t*-tests compared values inside and outside the exclosures, but given the lack of replication of sites, the *t*-tests could not separate true grazing effects from any other site difference that may have covaried with the location of the exclosure fences. No site differences were obvious, so we expect the *t*-tests represent primarily the grazing effects. Each vegetation type happened to be present at two exclosure sites, so we were able to test for the effect of grazing among sites with a split plot ANOVA approach (grazing treatment within exclosure site). We also tested for the overall effect of grazing by a split plot ANOVA (split-plot effect for grazing replicated at three sites).

Results

Across all vegetation types in all exclosures, the bulk density of the 0–15 cm depth mineral soil was higher in grazed units (0.94 kg/L; Table 1) than in ungrazed units (0.86 kg/L; $P = 0.04$). The pattern of greater bulk density on grazed units was strongest at exclosure 3, where the bulk density in the outside (grazed) area was 0.96 kg L, compared with 0.77 kg/L inside the exclosure. The mesic meadow vegetation type showed a greater difference in bulk density at exclosure 3 than did the aspen type. Despite the overall effect of higher bulk density in grazed units, the rocky upland sagebrush type showed no trend (Table 1).

No overall effect of grazing on pH was apparent across the exclosures and vegetation types, but grazing significantly affected soil pH in the aspen vegetation types (Table 1). This effect was consistent in both exclosures with aspen and was strongest at exclosure 3, where the 0–15 cm depth soil was 0.7 units lower inside the exclosure.

Grazing had no overall effect on total soil C and N across all exclosures and vegetation types (Table 2). The only significant effect among the vegetation types and exclosures was the mid-slope aspen type in exclosure 2, where the grazed area had 2.11 kg C/m^2 more C (to 30 cm) and 0.17 kg/m^2 more N than inside the exclosure. The effect of grazing in the aspen vegetation type at exclosure 3 was not significant (and was near 0), so we expect the large difference at exclosure 2 may result from site factors other than the effect of grazing.

The effects of grazing on soil cations and phosphorus were mixed. Grazing substantially reduced the quantities of extractable calcium, magnesium, potassium and phosphorus in the upland sagebrush type (Table 3), with average reductions of about one-third. The only other significant effect of grazing was higher extractable potassium in grazed aspen types.

Resin bags showed no overall effect of grazing through the growing season across all exclosures and vegetation types. The only significant effect was in exclosure 1, where net nitrification was three times higher with grazing than without (Table 4). Net N mineralization showed no significant effects of grazing treatments for individual communities within or across sites (Table 4). The resin estimates of N supply were generally higher for aspen than for upland sage or meadow, and net N mineralization also appeared higher for aspen.

No effects of grazing were evident in the soil solution concentrations in the wet meadow at exclosure 2 (Fig. 1), with both grazed and ungrazed units showing an average of about 0.10 mg N/L in springtime soil leachate. The effect of grazing appeared to be extremely large for the aspen vegetation type at exclosure 3, where the ungrazed unit with aspen trees averaged well under 1 mg N/L, compared with an average of nearly 5 mg N/L (mostly as nitrate) for the adjacent area where elk grazing has removed most of the aspen.

Table 1. Soil bulk density and pH by depth (means with standard deviations in parentheses).

Site #	Soil property by depth (cm)		Upland sagebrush		Mid-slope aspen		Lower-slope meadow		Site average	
			Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed
1	Bulk density	0–15	1.19 (0.10)	1.17 (0.13)					1.19 (0.10)	1.17 (0.13)
	(kg/L)	15–30	1.10 (0.21)	1.21 (0.25)					1.10 (0.21)	1.21 (0.25)
	pH	15	6.6 (0.2)	6.6 (0.3)					6.6 (0.2)	6.6 (0.3)
		15–30	6.7 (0.1)	6.7 (0.1)					6.7 (0.1)	6.7 (0.1)
2	Bulk density	0–15	1.02 (0.14)	1.04 (0.18)	0.82 (0.14)	0.90 (0.14)	0.68 (0.23)	0.64 (0.33)	0.84 (0.22)	0.86 (0.29)
	(kg/L)	15–30	1.03 (0.19)	1.10 (0.27)	0.99 (0.16)	1.02 (0.19)	0.82 (0.16)	0.92 (0.11)	0.95 (0.19)	1.02 (0.21)
	pH	0–15	6.3 (0.2)	6.4 (0.2)	6.1 (0.2)	6.2 (0.6)	5.9 (0.3)	5.6 (0.3)	6.1 (0.3)	6.1 (0.5)
		15–30	6.4 (0.3)	6.4 (0.4)	6.1 (0.2)	6.4 (0.4)	5.8 (0.3)	5.6 (0.4)	6.1 (0.4)	6.1 (0.5)
3	Bulk density	0–15			0.83 (0.17)[a]	0.94 (0.12)[a]	0.70 (0.26)[a]	0.98 (0.15)[a]	0.77 (0.22)[a]	0.96 (0.14)[a]
	(kg/L)	15–30			1.00 (0.18)	0.96 (0.14)	0.88 (0.33)	0.96 (0.28)	0.94 (0.27)	0.96 (0.22)
	pH	0–15			5.4 (0.1)[a]	6.1 (0.3)[a]	6.3 (0.2)[a]	6.5 (0.0)[a]	5.8 (0.5)[a]	6.3 (0.3)[a]
		15–30			5.2 (0.2)[a]	6.2 (0.3)[a]	6.3 (0.1)[a]	6.5 (0.1)[a]	5.7 (0.6)[a]	6.3 (0.3)[a]
Vegetation type average										
	Bulk density	0–15	1.11 (0.15)	1.10 (0.17)	0.82 (0.15)	0.92 (0.15)	0.69 (0.24)[a]	0.81 (0.31)[a]	0.86 (0.25)[a]	0.94 (0.25)[a]
	(kg/L)	15–30	1.06 (0.20)	1.15 (0.26)	1.00 (0.17)	0.99 (0.16)	0.86 (0.26)	0.94 (0.26)	0.97 (0.22)	1.03 (0.23)
	pH	0–15	6.5 (0.2)	6.5 (0.3)	5.7 (0.4)[a]	6.2 (0.5)[a]	6.1 (0.3)	6.0 (0.5)	6.1 (0.4)	6.2 (0.5)
		15–30	6.6 (0.3)	6.5 (0.4)	5.6 (0.5)[a]	6.3 (0.3)[a]	6.1 (0.3)	6.1 (0.6)	6.1 (0.5)	6.3 (0.5)

[a] $P < 0.1$.

Table 2. Total soil C and N (kg/m^2) by depth (means with standard deviations in parentheses).

Site #	Element	Soil depth (cm)	Upland sagebrush		Mid-slope aspen		Lower-slope meadow		Site average	
			Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed
1	C	0–15	1.81 (0.84)	1.78 (0.63)					1.81 (0.84)	1.78 (0.63)
		15–30	3.60 (1.00)	3.11 (0.88)					3.60 (1.00)	3.11 (0.88)
		0–30	5.41 (1.53)	4.90 (1.47)					5.41 (1.53)	4.90 (1.47)
	N	0–15	0.14 (0.06)	0.14 (0.05)					0.14 (0.06)	0.14 (0.05)
		15–30	0.30 (0.09)	0.27 (0.08)					0.30 (0.09)	0.27 (0.08)
		0–30	0.44 (0.13)	0.41 (0.12)					0.44 (0.13)	0.41 (0.12)
2	C	0–15	1.71 (0.39)	1.62 (0.58)	5.08 (1.94)[a]	6.48 (1.38)[a]	6.18 (2.06)	6.51 (1.12)	4.69 (2.17)	5.28 (2.06)
		15–30	2.81 (0.79)	2.86 (0.83)	3.85 (1.35)	4.56 (0.86)	4.04 (1.01)[a]	4.98 (1.30)[a]	3.20 (1.44)	3.72 (1.78)
		0–30	4.53 (0.84)	4.48 (1.10)	8.93 (2.83)[a]	11.04 (1.67)	10.22 (1.87)	11.49 (1.86)	7.89 (3.15)	9.00 (3.60)
	N	0–15	0.14 (0.04)	0.12 (0.04)	0.40 (0.15)[a]	0.51 (0.12)[a]	0.52 (0.17)	0.52 (0.11)	0.38 (0.18)	0.42 (0.17)
		15–30	0.23 (0.06)	0.24 (0.09)	0.31 (0.13)	0.37 (0.06)	0.37 (0.12)	0.48 (0.18)	0.28 (0.14)	0.32 (0.18)
		0–30	0.36 (0.06)	0.36 (0.11)	0.71 (0.23)[a]	0.88 (0.14)[a]	0.89 (0.17)	1.00 (0.18)	0.65 (0.27)	0.75 (0.32)
3	C	0–15			6.84 (1.24)	6.39 (1.33)	3.96 (1.78)	4.34 (0.97)	5.40 (2.10)	5.37 (1.54)
		15–30			3.44 (1.22)	3.94 (1.53)	3.15 (1.90)	2.38 (0.94)	3.30 (1.56)	3.16 (1.47)
		0–30			10.28 (1.36)	10.33 (2.77)	7.12 (3.45)	6.72 (1.62)	8.70 (3.02)	8.52 (2.88)
	N	0–15			0.54 (0.10)	0.48 (0.09)	0.32 (0.13)	0.33 (0.08)	0.43 (0.16)	0.41 (0.11)
		15–30			0.25 (0.10)	0.31 (0.12)	0.25 (0.16)	0.16 (0.07)	0.25 (0.13)	0.23 (0.12)
		0–30			0.80 (0.13)	0.79 (0.20)	0.57 (0.27)	0.50 (0.13)	0.68 (0.24)	0.64 (0.22)
Vegetation type average										
	C	0–15	3.21 (0.96)	2.99 (0.84)	5.96 (1.82)	6.43 (1.32)	5.07 (2.19)	5.43 (1.51)	4.75 (2.06)	4.95 (1.91)
		15–30	1.76 (0.64)	1.71 (0.60)	3.64 (1.27)	4.25 (1.25)	3.60 (1.55)	3.68 (1.73)	3.00 (1.48)	3.21 (1.67)
		0–30	4.97 (1.28)	4.69 (1.28)	9.60 (2.27)	10.68 (2.26)	8.67 (3.13)	9.10 (2.98)	7.75 (3.07)	8.16 (3.40)
	N	0–15	0.26 (0.09)	0.25 (0.08)	0.47 (0.14)	0.49 (0.10)	0.42 (0.18)	0.43 (0.14)	0.39 (0.16)	0.39 (0.15)
		15–30	0.14 (0.05)	0.13 (0.05)	0.28 (0.12)	0.34 (0.10)	0.31 (0.15)	0.32 (0.21)	0.24 (0.13)	0.26 (0.16)
		0–30	0.40 (0.11)	0.39 (0.11)	0.75 (0.19)	0.83 (0.18)	0.73 (0.28)	0.75 (0.30)	0.63 (0.26)	0.66 (0.29)

[a] $P < 0.1$.

Table 3. Extractable calcium, magnesium, potassium, and phosphorus (means with standard deviations in parentheses).

Site #	Cations (mmol/$_c$/m^2) and Bray-1 P (g/m^2)	Upland sagebrush		Mid-slope aspen		Lower-slope meadow		Site average	
		Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed
1	Calcium	6.3 (2.5)	4.6 (2.4)					6.3 (2.5)	4.6 (2.4)
	Magnesium	1.1 (0.4)	0.7 (0.4)					1.1 (0.4)	0.7 (0.4)
	Potassium	0.57 (0.16)	0.36 (0.21)					0.57 (0.16)	0.36 (0.21)
	Phosphorus	3.4 (2.2)[a]	1.9 (1.2)[a]					3.4 (2.2)[a]	1.9 (1.2)[a]
2	Calcium	6.5 (1.3)[a]	2.8 (2.2)[a]	13.4 (8.1)	11.3 (8.3)	13.0 (8.1)	16.1 (6.4)	10.9 (7.2)	10.4 (7.9)
	Magnesium	1.4 (0.2)[a]	0.7 (0.4)[a]	5.0 (3.5)	3.4 (2.5)	3.7 (2.3)	3.8 (1.5)	3.3 (2.8)	2.7 (2.2)
	Potassium	0.4 (0.1)	0.3 (0.2)	0.61 (0.30)	0.71 (0.36)	0.71 (0.33)	0.92 (0.40)	0.58 (0.29)	0.65 (0.41)
	Phosphorus	1.3 (1.4)[a]	0.1 (0.3)[a]	0.04 (0.13)	0.54 (1.46)	<0.01	<0.01	0.45 (0.97)	0.24 (0.86)
3	Calcium			12.5 (3.9)	13.8 (3.6)	11.4 (2.6)	11.5 (4.1)	12.0 (3.3)	12.6 (4.0)
	Magnesium			3.8 (1.3)	3.1 (1.0)	2.2 (0.8)	2.0 (0.7)	3.1 (1.3)	2.5 (1.0)
	Potassium			0.85 (0.27)[a]	1.34 (0.51)[a]	1.18 (0.51)	0.90 (0.49)	1.01 (0.42)	1.12 (0.54)
	Phosphorus			0.03 (0.08)	0.45 (1.42)	3.1 (2.9)	4.7 (4.1)	1.56 (2.53)	2.59 (3.72)
Landscape average									
	Calcium	6.4[a]	4.2[a]	13.0	12.6	12.2	13.8	10.5	10.2
	Magnesium	1.2[a]	0.7[a]	4.4	3.2	3.0	2.9	2.9	2.3
	Potassium	0.50[a]	0.33[a]	0.73[a]	1.04[a]	0.95	0.91	0.72	0.76
	Phosphorus	2.4[a]	1.0[a]	0.03	0.50	1.55	2.37	1.31	1.29

[a] $P < 0.01$.

Table 4. Annual resin-bag N and net N mineralizations (means with standard deviations in parentheses).

Site #	Resin-N (mg/bag), or net mineralization (g N/m^2)	Upland sagebrush		Mid-slope aspen		Lower-slope meadow		Site average	
		Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed
1	Resin NH_4-N	7.3 (9.0)	7.8 (7.5)					7.3 (9.0)	7.8 (7.5)
	Resin NO_3-N	3.2 (2.8)[a]	10.5 (7.3)[a]					3.2 (2.8)[a]	10.5 (7.3)[a]
	Resin sum	10.5 (10.2)	18.3 (13.5)					10.5 (10.2)	18.3 (13.5)
	Net N min.	3.8 (5.0)	3.8 (2.4)					3.8 (5.0)	3.8 (2.4)
2	Resin NH_4-N	5.2 (2.8)	4.1 (0.8)	10.0 (19.6)	5.8 (4.2)	5.0 (2.8)	2.8 (2.5)	6.7 (11.4)	4.5 (3.2)
	Resin NO_3-N	4.5 (4.3)	4.3 (2.6)	13.2 (29.4)	7.6 (5.5)	3.1 (0.7)	4.6 (2.6)	6.9 (17.1)	6.2 (5.2)
	Resin sum	9.7 (5.2)	8.4 (2.9)	23.2 (48.6)	13.3 (7.2)	8.0 (2.6)	7.4 (2.4)	13.7 (28.0)	10.6 (6.7)
	Net N min.	2.5 (1.0)	3.0 (1.6)	5.9 (4.2)	7.2 (8.2)	2.9 (1.8)	6.0 (7.8)	3.8 (3.0)	4.6 (5.2)
3	Resin NH_4-N			11.7 (15.9)	9.1 (9.1)	2.7 (1.6)	2.7 (1.6)	5.2 (6.3)	7.2 (11.9)
	Resin NO_3-N			6.7 (4.5)	6.8 (3.8)	4.8 (2.3)	3.5 (2.2)	4.8 (3.2)	5.7 (3.6)
	Resin sum			18.4 (18.6)	16.0 (12.7)	7.6 (2.7)	6.2 (1.9)	10.0 (9.0)	13.0 (14.1)
	Net N min.			6.1 (5.9)	7.9 (5.0)	6.2 (5.3)	3.7 (1.5)	6.2 (5.4)	5.6 (4.1)
Landscape average									
	Resin NH_4-N	6.2	5.9	10.9	7.1	3.8	2.8	7.0	5.1
	Resin NO_3-N	3.9	7.4	9.9	7.3	4.0	4.0	6.0	6.2
	Resin sum	10.1	13.4	20.8	14.4	7.8	6.8	13.0	11.3
	Net N min.	3.1	3.4	6.0	7.5	4.6	4.9	4.3	5.0

[a]$P < 0.01$.

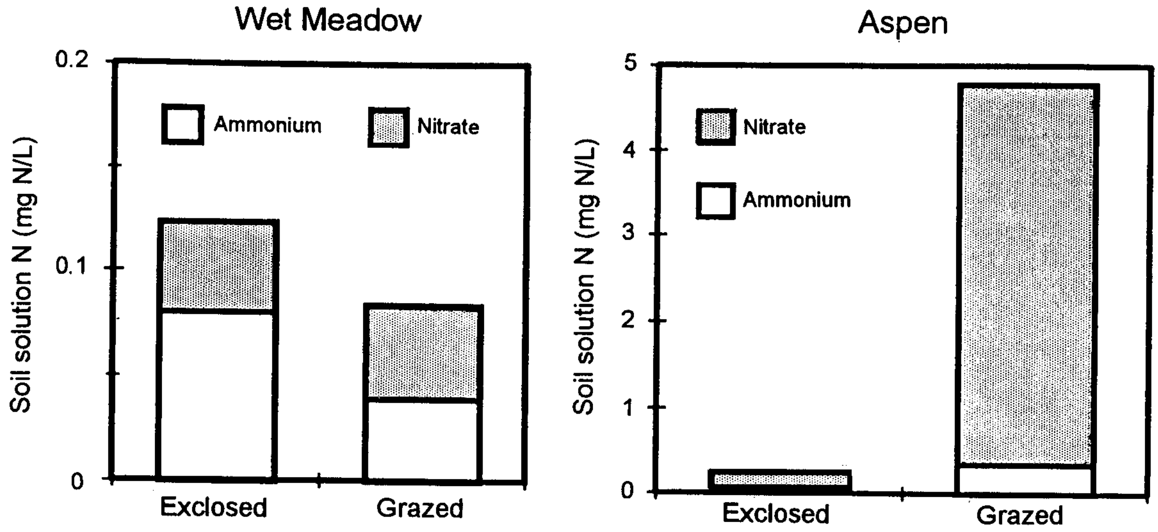

Fig. 1. Average (4 sampling periods at 2-week intervals in spring 1999) concentrations of ammonium-N and nitrate N in soil solutions sampled at 30–35 cm depth with ceramic cup tension lysimeters. No effect of grazing was apparent for the wet meadow site, but at the aspen site grazing substantially increased nitrate leaching (P <0.03) and ammonium+nitrate leaching (P <0.02).

Fertilization with N doubled the production of grasses (Fig. 2) and shrubs (Fig. 3), indicating that current productivity in these ecosystems are strongly N limited. The fertilization treatments showed no interaction with grazing (P <0.5), so the N limitation on growth was not alleviated or exacerbated by grazing.

Discussion

The major effects of high elk populations in our study sites appear to be an increase in soil bulk density with grazing (except for the rocky upland sagebrush type), and an increase in soil pH with grazing of aspen vegetation types. We did not assess the direct cause of the lower pH under aspen, but given similar soil C and extractable cation concentrations, we expect the difference likely results from the accumulation of more-strongly acidic organic matter under aspen (Binkley et al. 1989). The total quantity of C and N stored in soils did not differ across the exclosures and vegetation types, with one exception (exclosure 2 aspen type), so we conclude there was no evidence of substantial effects of elk grazing on soil C and N. Grazing lowered the extractable quantities of base cations and phosphorus in the upland sagebrush soils, but not in the other soils. The resin bags and net N mineralization assays showed no strong effects of grazing.

These findings contrast somewhat with those of Frank and Groffman (1998) for seven exclosures in grassland sites in Yellowstone National Park. They found no effect of grazing on 0–10 cm depth soil bulk density, soil C, or soil N, but a consistently higher rate of net N mineralization from grazed areas. Lane and Montagne (1996) also examined these exclosures, and concluded that grazing increased the bulk density of the 0–5 cm depth soil by 30%. In Rocky Mountain National Park, elk grazing and hoof action compacted soils at two of the three sites, particularly in the grass type. Our single case of significant differences in soil C and N came from an aspen-dominated vegetation type, which was not represented in the Yellowstone study. Interestingly, the annual rates of net N mineralization were similar between the studies, ranging from 2.5 to 7.2 gN m^{-2} yr^{-1} for Rocky Mountain (average 4.7 gN m^{-2} yr^{-1}), and between 0.9 and 8.1 gN m^{-2} yr^{-1} for Yellowstone (average 3.0 gN m^{-2} yr^{-1}). The biggest difference between the two studies was in the rates of net N mineralization. The incubation methods differed slightly with the Yellowstone study using soils in plastic bags rather than tubes, but this should not introduce any major artifact. Our Rocky Mountain

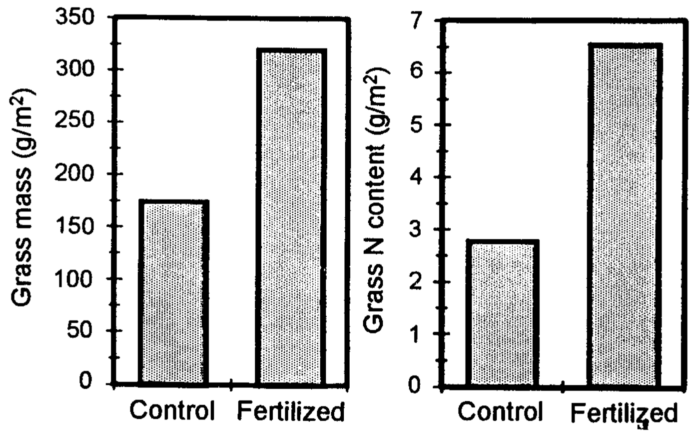

Fig. 2. Average mass and N content of grasses (with some herbs) in 0.25 m^2 plots with and without N fertilization (P <0.1 for mass, P <0.05 for N content; effect of grazing not significant).

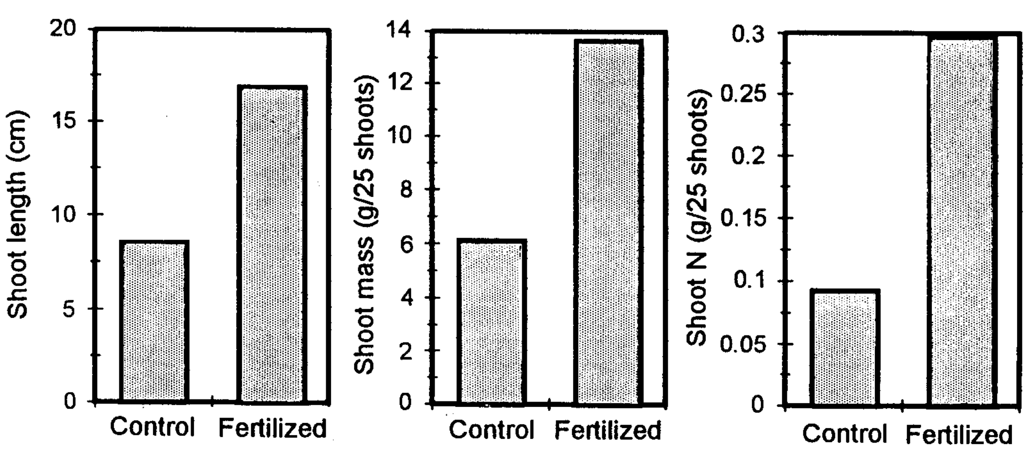

Fig. 3. Average shoot length, shoot mass and N content (total of 25 shoots/shrub) with and without N fertilization (P <0.02 for length, P <0.05 for mass, P <0.1 for N content; effect of grazing not significant).

study used longer cores (0–15 cm, rather than 0–10 cm), which might increase the Rocky Mountain values relative to Yellowstone. The effect of grazing on net N mineralization was clear for the Yellowstone study, but no substantial effect was evident in our Rocky Mountain study. Given the similarity of approaches, we expect this difference in pattern between the two national parks probably represents a real difference in the effect of grazing rather than artifacts of the methods.

Why should the effects of elk grazing differ among vegetation types in Rocky Mountain National Park and between this park and Yellowstone National Park? No simple answers are available, and given that the much larger literature on livestock grazing shows the same inconsistent stories (Milchunas and Lauenroth 1993; Burke et al. 1997), we expect the real effects of grazing have real differences across vegetation types and locations. Important factors that influence the effect of grazing on a particular location might include the actual intensity of grazing (across years), the particular species present, any changes in vegetation composition, and the properties and dynamics of the soil.

The apparent effect of grazing on soil N leaching at exclosure 2 in the aspen vegetation type was surprisingly large. The differences in soil solution concentrations were consistent among lysimeters and across sampling dates, so we are confident the pattern was real. However, without replication of the exclosures, these real differences could result either from grazing or from site factors. Unfortunately, other studies have not examined soil leachates with respect to grazing exclosures, so we cannot say if our findings are representative or unusual.

Overall, the only clear effects of high elk populations in our study were: (1) higher soil bulk density (except for rockier, upland sage communities); and (2) lower extractable base cations and phosphorus in upland sagebrush sites, and higher soil pH where elk grazing prevented aspen growth. Grazing also appeared to have a large effect on nitrate leaching losses for the aspen type at exclosure 3, but without replication of sites we remain unsure about the contribution of grazing or site effects. We found no other clear evidence of major impacts of heavy elk grazing on soil N supply or overall accumulation of total N and C in the soil, and without such changes, we conclude there is no evidence of a substantial effect of elk on sustainability of soil fertility. We found no reason to speculate that any major decrease in elk populations would have major effects on soils. Any potential effect of large increases in elk populations would be difficult to predict, and we would not be confident in concluding that no soil changes would result. Our fertilization treatments clearly showed that the availability of N strongly limits plant growth, so we expect that any future development of grazing effects on N supply would have important implications for plant species composition and growth.

We stress that three large exclosures may not be enough to identify any effects except very large ones, and that more subtle effects might be apparent over longer time periods, or with stronger experimental designs (such as more replicate exclosures). A new suite of 16 exclosures was established in 1994; if these are maintained for several decades, they may provide a strong enough design to identify the effects of elk grazing on soils and nutrient cycling more definitively.

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Literature Cited

Adams, M. A., and P. M. Attiwill. 1986. Nutrient cycling and nitrogen mineralization in eucalypt forests of southeastern Australia. II. Indices of nitrogen mineralization. Plant and Soil 92:341–362.

Baker, W. L., J. A. Munroe, and A. E. Hessl. 1997. The effect of elk on aspen in the winter range of Rocky Mountain National Park, Colorado, USA. Ecography 20:155–165.

Bazely, D. R., and R. L. Jefferies. 1985. Goose feces: A source of nitrogen for plant growth in a grazed salt marsh. Journal of Applied Ecology 22:693–703.

Binkley, D., and S. C. Hart. 1989. The components of nitrogen availability assessments in forest soils. Advances in Soil Science 10:57–116.

Binkley, D., C. T. Driscoll, H. L. Allen, P. Schoeneberger, and D. McAvoy. 1989. Acidic deposition and forest soils. Springer-Verlag, New York.

Burke, I. C., W. K. Lauenroth, and D. G. Milchunas. 1997. Biogeochemistry of managed grasslands in central North America. Pages 85–102 *in* E. Paul, K. Paustian, E. Elliott, and C. Cole, editors. Soil organic matter in temperate agroecosystems. CRC Press, Boca Raton, Fla.

Caughley, G. 1981. Pages 6–9 *in* P. A. Jewell and S. Holt, editors. Problems in management of locally abundant wild mammals. Academic Press, Orlando, Fla.

Caughley, G., and J. H. Lawton 1981. Plant-herbivore systems. Pages 132–166 *in* R. M. May, editor. Theoretical ecology. 2e. Blackwell Scientific, Oxford.

Coughenour, M. B. 1991. Biomass and nitrogen responses to grazing of upland steppe on Yellowstone's northern winter range. Journal of Applied Ecology 28:71–82.

Coughenour, M. B., and F. J. Singer. 1995. Yellowstone elk population responses to fire: Landscape carrying capacity and spatial ecosystem modeling. Pages 169–180 *in* J. M. Greenlee, editor. Ecological implications of fire in Greater Yellowstone. International Association of Wildland Fire, Fairfield, Wash.

Ellis, J. E., and D. M. Swift. 1988. Stability of African pastoral ecosystems: Alternative paradigms and implications for development. Journal of Range Management 41:450–459.

Frank, D. A., and P. M. Groffman. 1998. Ungulate vs. landscape control of soil C and N processes in grasslands of Yellowstone National Park. Ecology 79:2229–2241.

Frank, D. A., and S. J. McNaughton. 1992. The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. Ecology 73:2043–2058.

Fuls, E. R. 1992. Ecosystem modification created by patch-overgrazing in semi-arid grassland. Journal of Arid Environments 23:59–69.

Gordon, I. J. 1988. Facilitation of red deer grazing by cattle and its impact on red deer performance. Journal of Applied Ecology 25:1–10.

Holland, E. A., and J. K. Detling. 1990. Plant response to herbivory and belowground nitrogen cycling. Ecology 71:1040–1049.

Iason, G. R., D. C. Duck, and T. H. Clutton-Brock. 1986. Grazing and reproductive success of red deer: The effects of local enrichment by gull colonies. Journal of Animal Ecology 55:507–515.

Knapp, A. K., and T. R. Seastedt. 1986. Detritus accumulation limits production of tallgrass prairie. BioScience 36:662–668.

Lane, J. R., and C. Montagne. 1996. Characterization of soils from grazing exclosures and adjacent areas in northern Yellowstone National Park. Pages 63–71 *in* F. Singer, editor. Effects of grazing by wild ungulates in Yellowstone National Park. U.S. Department of the Interior, National Park Service Technical Report NPS/96-01.

McNaughton, S. J. 1983. Grazing lawns: Animals in herds, plant form, and coevolution. American Naturalist 124:863–886.

McNaughton, S. J. 1988. Mineral nutrition and spatial concentration of African ungulates. Nature 334:343–345.

McNaughton, S. J. 1990. Mineral nutrition and seasonal movement of African ungulates. Nature 345:613–615.

Milchunas, D. G., and W. K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs 63:327–366.

Moss, R., D. Welch, and P. Rothery. 1981. Effects of grazing by mountain hares and red deer on the production and chemical composition of heather. Journal of Applied Ecology 18:487–496.

Mould, E. D., and C. T. Robbins. 1981. Nitrogen metabolism in elk. Journal of Wildlife Management 45:323–334.

Risser, P. G., and W. J. Parton. 1982. Ecosystem analysis of the tallgrass prairie: Nitrogen cycle. Ecology 63:1342–1351.

Seagle, S. W., and S. J. McNaughton. 1992. Simulated effects of grazing on soil nitrogen and mineralization in contrasting Serengeti grassland. Ecology 73:1105–1111.

Singer, F. J. 1995. Effects of grazing by ungulates on upland bunchgrass communities of the northern range of Yellowstone National Park. Northwest Science 69:191–203.

Singer, F. J., and M. K. Harter. 1996. Comparative effects of elk herbivory and fires of 1988 on grasslands in northern Yellowstone National Park. Ecological Applications 6:185–199.

Suzuki, K., H. Suzuki, D. Binkley, and T. Stohlgren. 1999. Aspen regeneration in the Colorado Front Range: Differences at local and landscape scales. Landscape Ecology 14:231–237.

U.S. Department of Agriculture, Natural Resources Conservation Service. 1996. Pages 327–331 *in* Soil Survey Laboratory Methods Manual. Soil Survey Investigations Report No. 42, Version 3.0.

Wagner, F. H., R. Foresta, R. B. Gill, D. R. McCullough, R. R. Pelton, W. F. Porter, and H. Salwasser. 1995. Wildlife policies in the U.S. national parks. Island Press, Washington D.C. 242 pp.